# Trail-following bacteria:
## from single particle dynamics to collective behaviour

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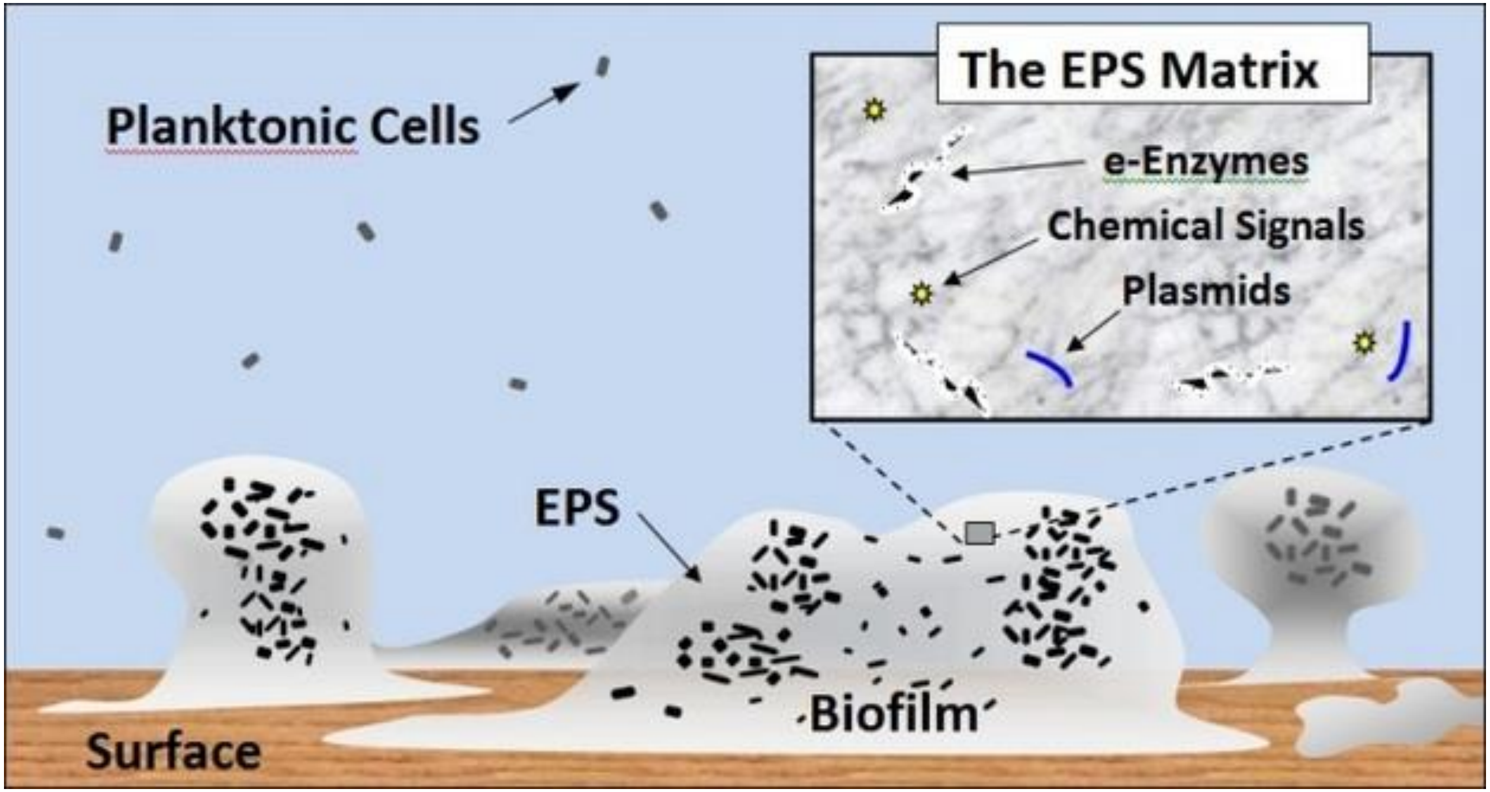
# Biofilms: Strongly Correlated Systems

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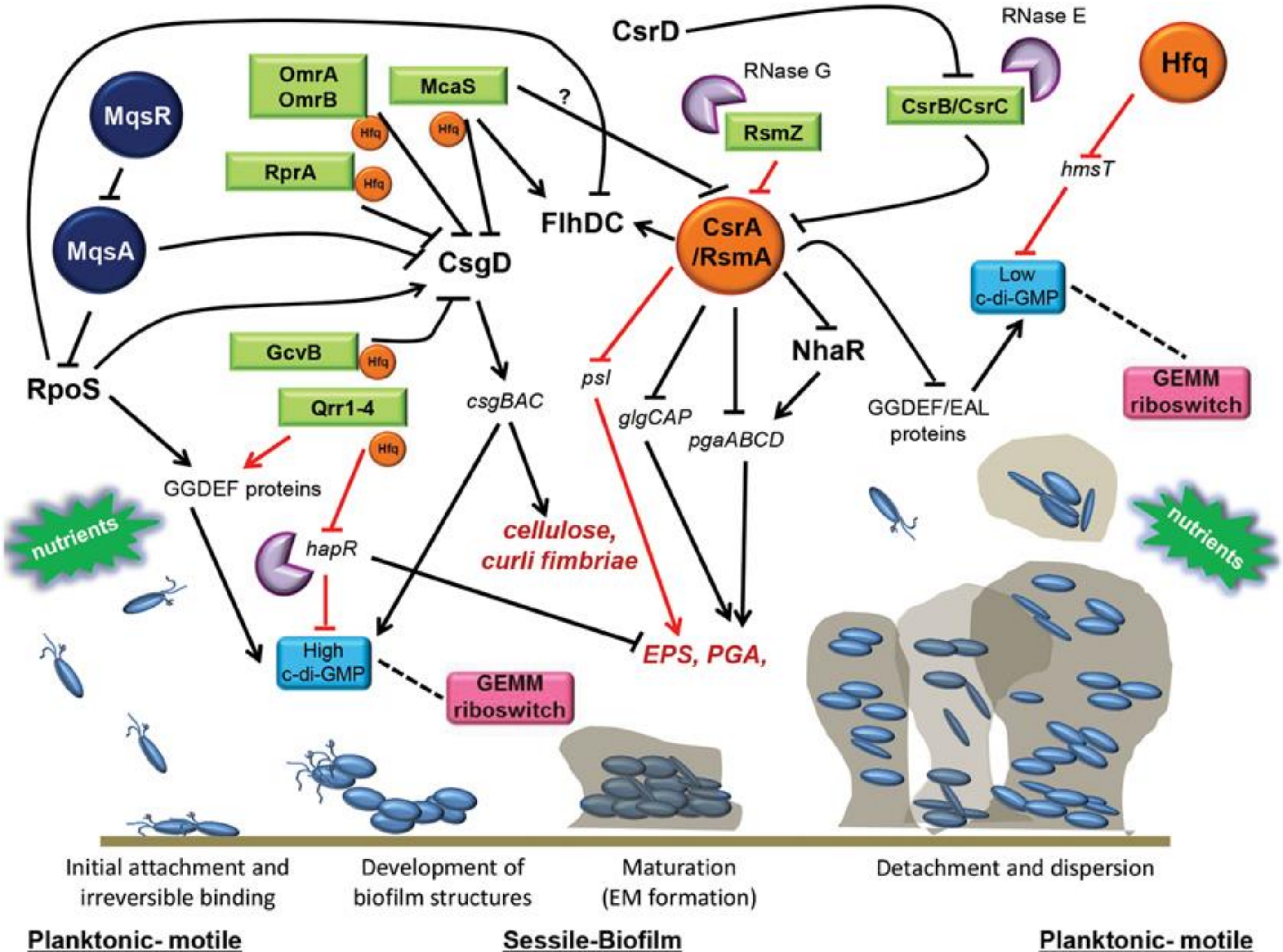
► **how do the bacteria achieve this self-organization?**

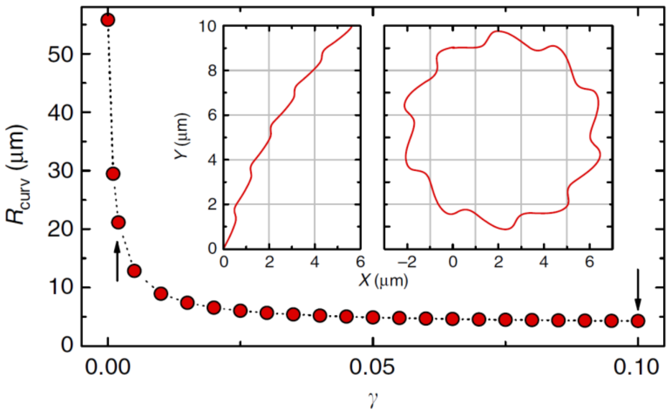
# From Molecules to Systems

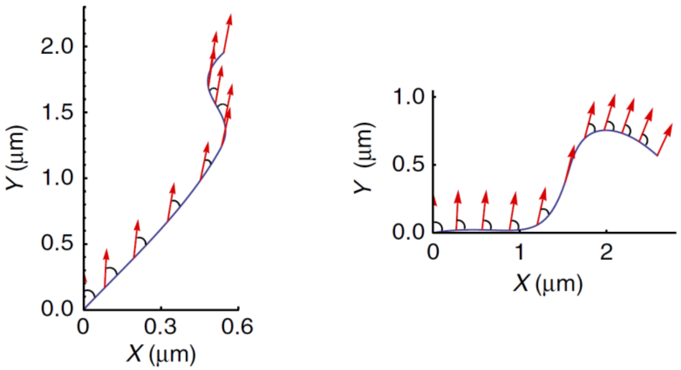


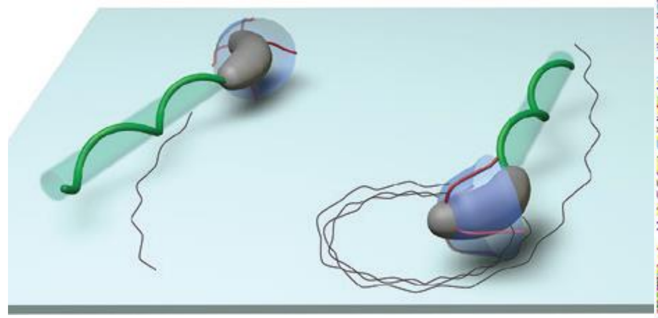

Front. Cell. Infect. Microbiol., 25 March 2014 http://dx.doi.org/10.3389/fcimb.2014.00038

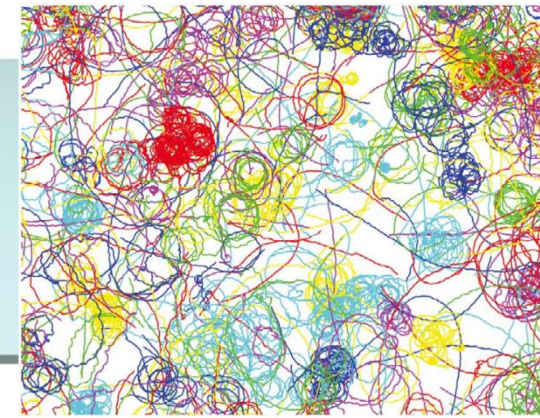
# Bacteria Swimming near Surface

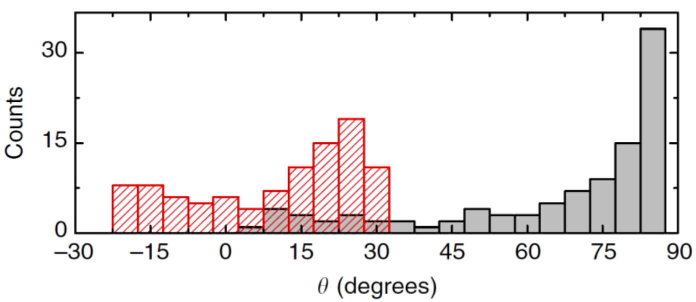
- **pili friction leads to modulation**
- **modulation allows control**
- **high friction: orbiting**
- **low friction: roaming**



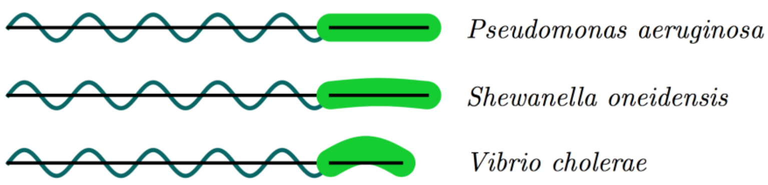




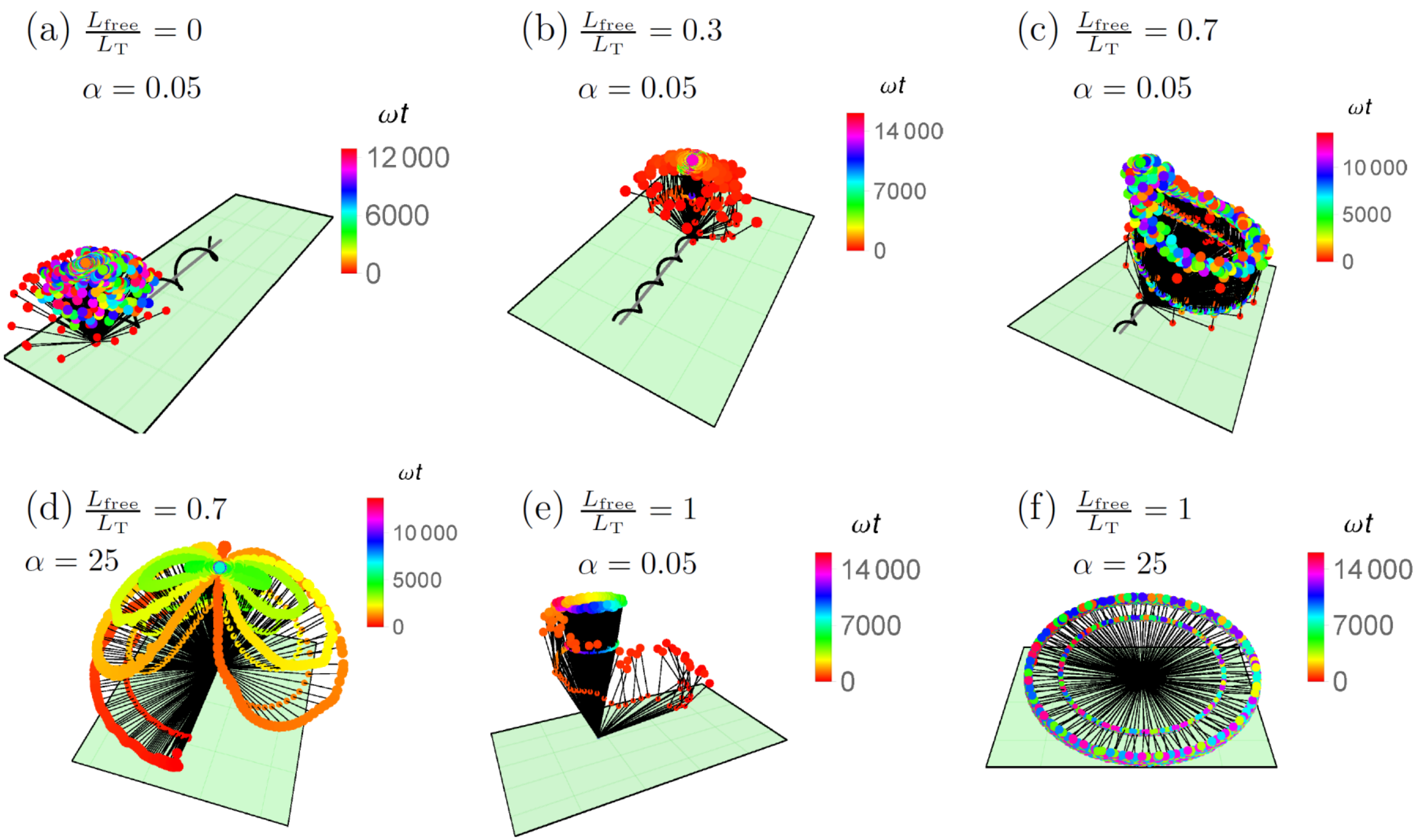

orbiting roaming

A.S. Utada, R.R. Bennett, J.C.N. Fong, M.L. Gibiansky, F.H. Yildiz, R. Golestanian, and G.C.L. Wong, Nat Commun **5**, 4913 (2014)

# Bacteria Conformation on Surface

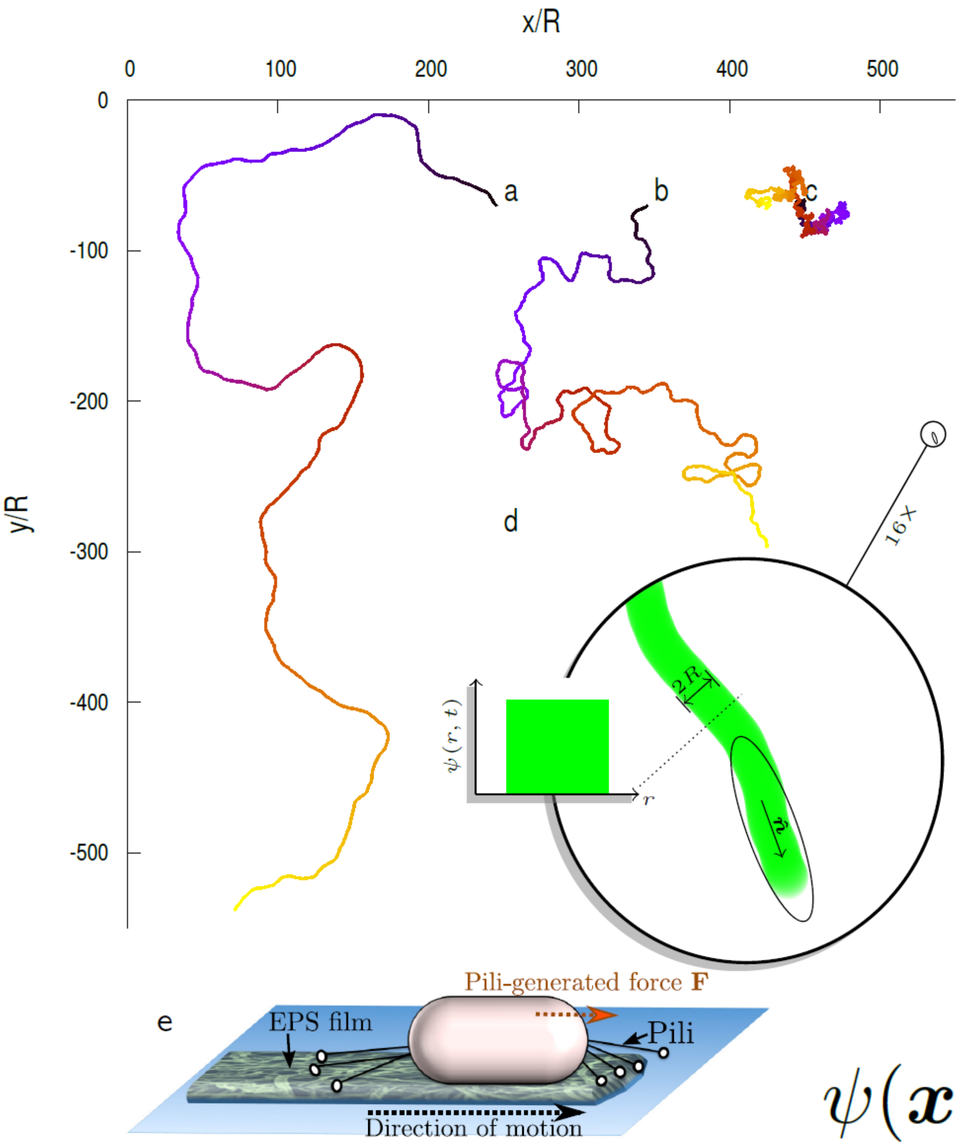



- **degree of attachment**
- **elasticity of hook**
- **shape**




R.R. Bennett, C.K. Lee, J. De Anda, K.H. Nealson, F.H. Yildiz, G.A. O'Toole, G.C.L. Wong, R. Golestanian, J R Soc Interface **13**, 20150966 (2016)

# Phenomenology of Trail-Mediated Interaction




## Chemotaxis without Diffusion

$$\psi(\boldsymbol{x},t) = k\int_0^t dt'\,\delta_R^2\left(\boldsymbol{x}-\boldsymbol{r}(t')\right)$$

W.T. Kranz, A. Gelimson, K. Zhao, G.C.L. Wong, and R. Golestanian, Phys Rev Lett **117,** 038101 (2016)

# Bacterial Chemotaxis and Quorum Sensing

## Nucleating early biofilm colonies

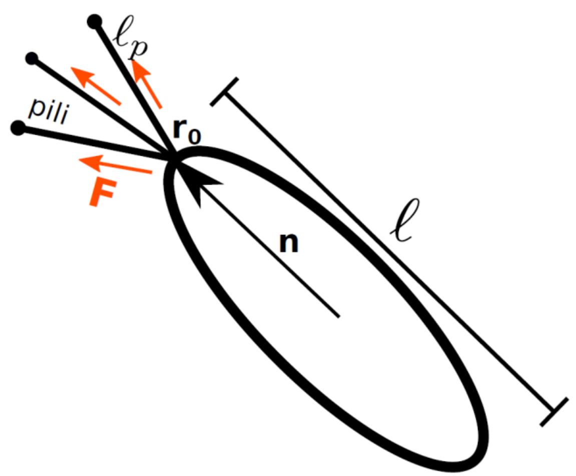
**Anatolij Gelimson**
*DPhil Student*
2012-2016

- **how is bacterial motility affected by EPS secretion?**
- **how does this control their collective behaviour?**

# Pili Driven Motility with EPS Interaction

$\Theta_i = 0$ **detached, with rate** $\mu(\psi_i)$

$\Theta_i = 1$ **attached, with rate** $\lambda(\psi_i)$




$$\boldsymbol{F} = \sum_i \hat{\boldsymbol{e}}_i f(\psi_i)\Theta_i$$

$$\psi_i = \psi(\boldsymbol{r}_0 + \ell_p \hat{\boldsymbol{e}}_i)$$

$$\psi_i = \psi(\boldsymbol{r}_0 + \ell_p \hat{\boldsymbol{e}}_i) \approx \psi(\boldsymbol{r}_0) + \ell_p (\boldsymbol{\nabla}\, \psi|_{\boldsymbol{r}_0} \cdot \hat{\boldsymbol{e}}_i)$$

$$\Theta_i = \bar{\Theta} + \delta\Theta_i$$

$$\boldsymbol{F} = \sum_i \hat{\boldsymbol{e}}_i f(\psi)\bar{\Theta}(\psi) + \sum_i \hat{\boldsymbol{e}}_i \ell_p (\boldsymbol{\nabla}\psi \cdot \hat{\boldsymbol{e}}_i)\partial_\psi (f\bar{\Theta}) + \sum_i \hat{\boldsymbol{e}}_i f(\psi_i)\delta\Theta_i$$

A. Gelimson, K. Zhao, C.K. Lee, W.T. Kranz, G.C.L. Wong, and R. Golestanian, Phys Rev Lett **117,** 178102 (2016)

# Pili Driven Motility with EPS Interaction

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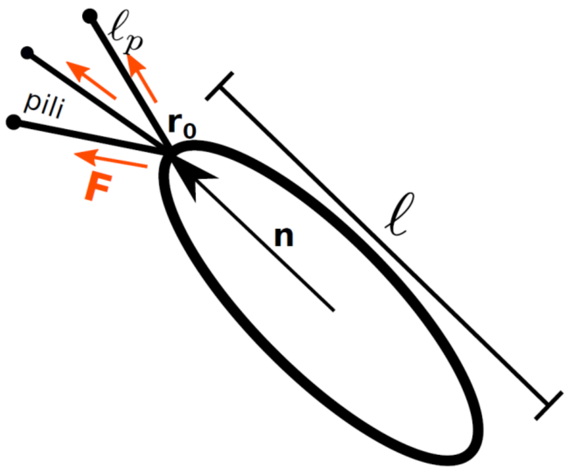



$$\bar{\Theta} = \langle \Theta_i \rangle = \frac{\lambda(\psi)}{\lambda(\psi) + \mu(\psi)}$$

$$\sigma^2 = \langle (\Theta_i - \bar{\Theta})^2 \rangle = \frac{\lambda(\psi)\mu(\psi)}{[\lambda(\psi) + \mu(\psi)]^2}$$

$$\langle \delta\Theta_i(t)\delta\Theta_i(t') \rangle = \frac{\sigma^2(\psi)}{[\lambda(\psi) + \mu(\psi)]}\delta_{ij}\delta(t - t')$$

A. Gelimson, K. Zhao, C.K. Lee, W.T. Kranz, G.C.L. Wong, and R. Golestanian, Phys Rev Lett **117,** 178102 (2016)

$$\frac{d\boldsymbol{r}}{dt} = \frac{1}{\gamma_{\|}} \boldsymbol{F}_{\|} + \frac{1}{\gamma_{\perp}} \boldsymbol{F}_{\perp} = v(\psi)\hat{\boldsymbol{n}} + A(\psi)(\boldsymbol{\nabla}\psi \cdot \hat{\boldsymbol{n}}_{\perp})\hat{\boldsymbol{n}}_{\perp} + B(\psi)(\boldsymbol{\nabla}\psi \cdot \hat{\boldsymbol{n}})\hat{\boldsymbol{n}} + \sqrt{2D_{\|}}\, \eta^{\|}\hat{\boldsymbol{n}} + \sqrt{2D_{\perp}}\, \eta^{\perp}\hat{\boldsymbol{n}}_{\perp}$$

$$\frac{d\hat{\boldsymbol{n}}}{dt} = -\hat{\boldsymbol{n}} \times \boldsymbol{\omega} = -\frac{1}{\gamma_{\mathrm{rot}}}\, \hat{\boldsymbol{n}} \times \boldsymbol{\tau} = -\chi(\psi)\hat{\boldsymbol{n}} \times [\hat{\boldsymbol{n}} \times \boldsymbol{\nabla}\psi] + \sqrt{2D_r(\psi)}\, \eta^{\perp}\hat{\boldsymbol{n}}_{\perp}$$

$$D_r(\psi) = \frac{N}{8}\langle \sin^2\vartheta_i \rangle \frac{\ell^2 f^2(\psi)}{\gamma_{\mathrm{rot}}^2} \frac{\lambda(\psi)\mu(\psi)}{[\lambda(\psi)+\mu(\psi)]^3}$$

$$v(\psi) = N\langle \cos\vartheta_i \rangle \frac{f(\psi)}{\gamma_{\|}} \frac{\lambda(\psi)}{\lambda(\psi)+\mu(\psi)}$$

$$D_{\|}(\psi) = \left[\frac{4\gamma_{\mathrm{rot}}^2 c_2}{\ell^2\gamma_{\|}^2(1-c_2)}\right] D_r(\psi),$$

$$D_{\perp}(\psi) = \left(\frac{2\gamma_{\mathrm{rot}}}{\gamma_{\perp}\ell}\right)^2 D_r(\psi),$$

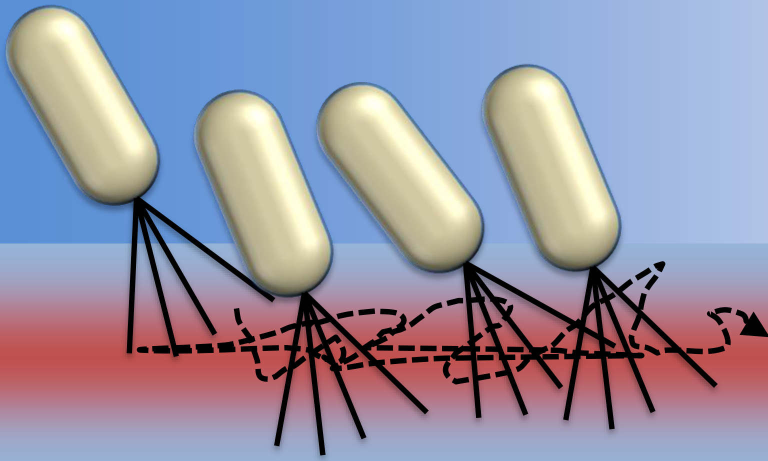
$$\chi(\psi) = \left[\frac{\gamma_{\|}\ell\ell_p(1-c_2)}{2\gamma_{\mathrm{rot}}c_1}\right]\partial_\psi v(\psi) + \alpha\partial_\psi D_r(\psi),$$

$$A(\psi) = \left[\frac{\ell_p(1-c_2)\gamma_{\|}}{c_1\gamma_{\perp}}\right]\partial_\psi v(\psi) + \alpha\left(\frac{2\gamma_{\mathrm{rot}}}{\gamma_{\perp}\ell}\right)^2\partial_\psi D_r(\psi),$$

$$B(\psi) = \left[\frac{\ell_p c_2}{c_1}\right]\partial_\psi v(\psi) + \alpha\left[\frac{4\gamma_{\mathrm{rot}}^2 c_2}{\ell^2\gamma_{\|}^2(1-c_2)}\right]\partial_\psi D_r(\psi),$$

**non-trivial dependence on psl concentration due to competing contributions**

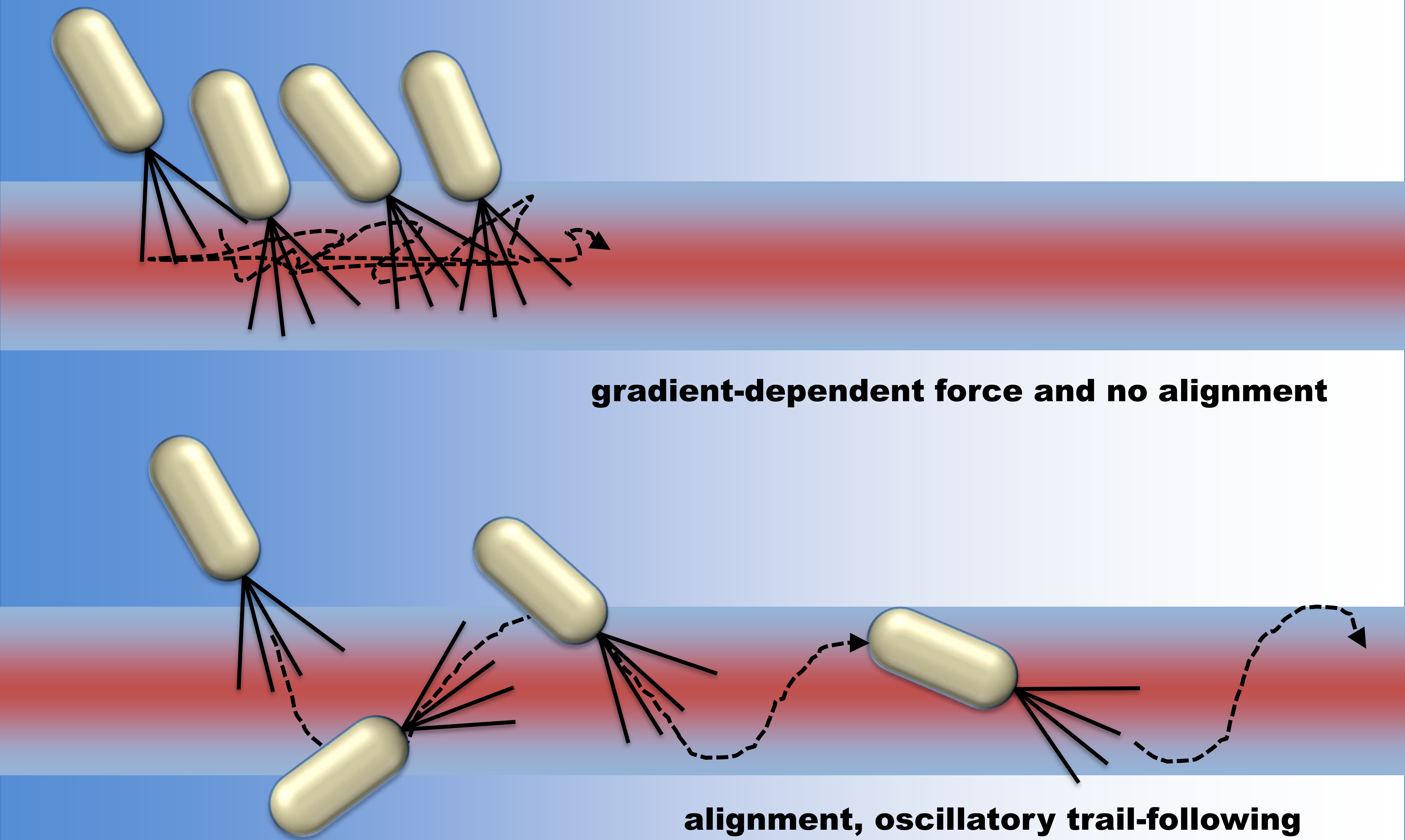
# How Can Bacteria Follow EPS Trails?



**gradient-dependent force and no alignment**

WT Kranz, A Gelimson, K Zhao, GCL Wong, and R Golestanian, Phys Rev Lett **117,** 038101 (2016)

# How Can Bacteria Follow EPS Trails?




WT Kranz, A Gelimson, K Zhao, GCL Wong, and R Golestanian, Phys Rev Lett **117,** 038101 (2016)

# Collective Behaviour

$$\frac{d\boldsymbol{r}_a}{dt} = A(\psi)\,(\boldsymbol{\nabla}\psi\cdot\hat{\boldsymbol{n}}_{\perp a})\,\hat{\boldsymbol{n}}_{\perp a} + B(\psi)\,(\boldsymbol{\nabla}\psi\cdot\hat{\boldsymbol{n}}_a)\,\hat{\boldsymbol{n}}_a + v(\psi)\,\hat{\boldsymbol{n}}_a + \sqrt{2D_{||}(\psi)}\,\eta_a^{||}\,\hat{\boldsymbol{n}}_a + \sqrt{2D_{\perp}(\psi)}\,\eta_a^{\perp}\,\hat{\boldsymbol{n}}_{\perp a}$$

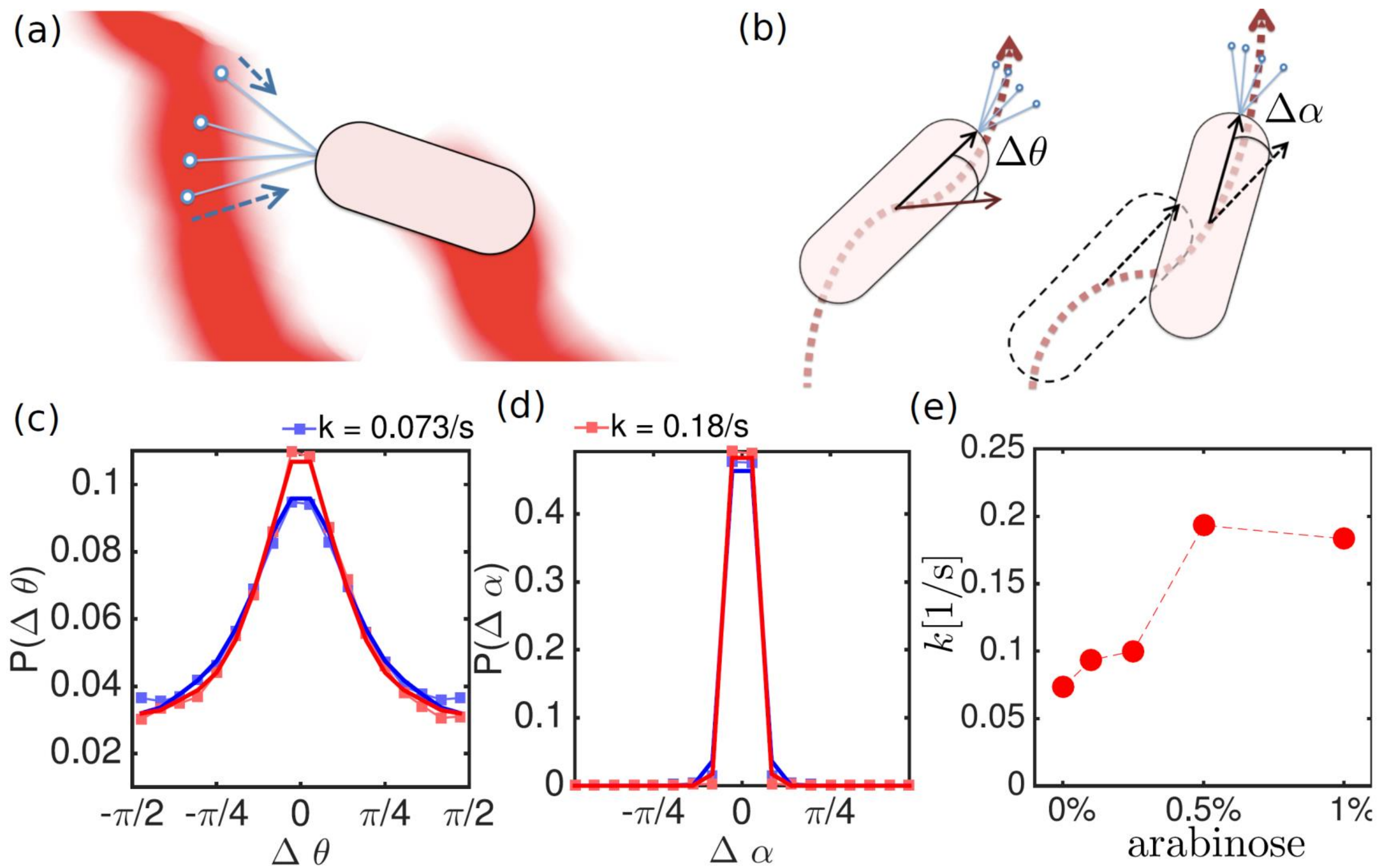
$$\frac{d\hat{\boldsymbol{n}}_a}{dt} = -\chi(\psi)\,\hat{\boldsymbol{n}}_a\times[\hat{\boldsymbol{n}}_a\times\boldsymbol{\nabla}\psi] + \sqrt{2D_r(\psi)}\,\eta_a^{\perp}\,\hat{\boldsymbol{n}}_{\perp a}$$

$$\partial_t\psi(\boldsymbol{r},t) = k\sum_a \frac{1}{2\pi\delta^2}\,e^{-(\boldsymbol{r}-\boldsymbol{r}_a)^2/2\delta^2}$$

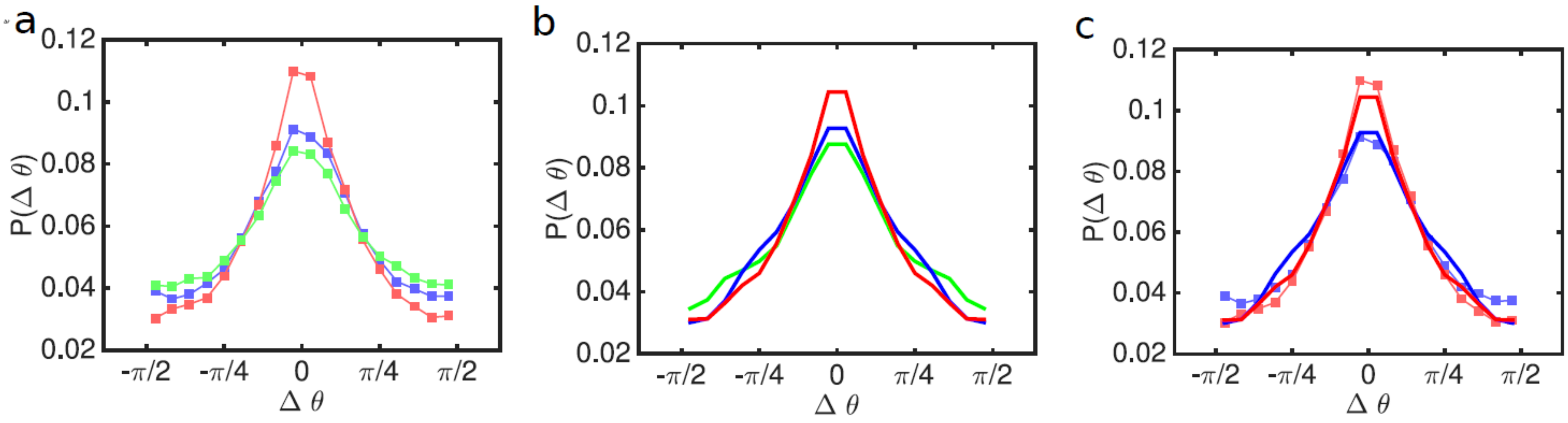
## Programme of Action

1. Extracting the parameters using single-bacterium experimental trajectories
2. **Predicting multicellular self-organization**
3. Comparing with experimental observations

# Characterizing the Motion of Single *P. aeruginosa*



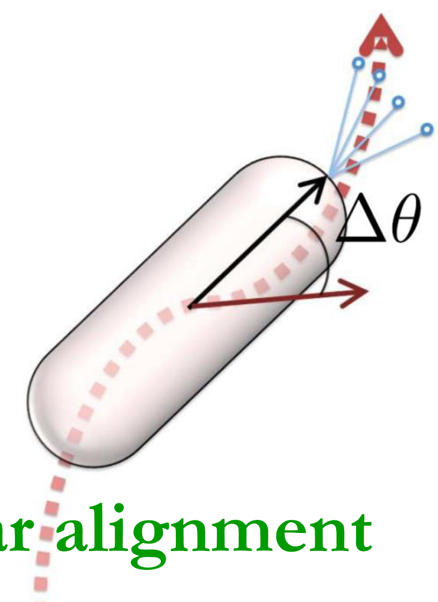
# Experimental Evidence for Perpendicular Alignment




experiment | theory | exp/theo agreement

$\Delta P_{psl}/P_{BAD}\text{-}psl$

**increasing psl concentration leads to narrowing of the orientation distribution without affecting the rotational diffusion**




▶ **this is only possible through perpendicular alignment**

# What do we learn from single *P. aeruginosa* results?

$$D_r(\psi) = \frac{N}{8} \langle \sin^2 \vartheta_i \rangle \frac{\ell^2 f^2(\psi)}{\gamma_{\mathrm{rot}}^2} \frac{\lambda(\psi)\mu(\psi)}{[\lambda(\psi)+\mu(\psi)]^3}$$

$$v(\psi) = N \langle \cos \vartheta_i \rangle \frac{f(\psi)}{\gamma_{||}} \frac{\lambda(\psi)}{\lambda(\psi)+\mu(\psi)}$$

non-trivial dependence on psl concentration due to competing contributions

- **Velocity increases when psl increases**
- **Rotational diffusion does not change when psl increases**

# What do we learn from single *P. aeruginosa* results?

$$D_r(\psi) = \frac{N}{8}\langle \sin^2 \vartheta_i \rangle \frac{\ell^2 f^2(\psi)}{\gamma_{\mathrm{rot}}^2} \frac{\lambda(\psi)\mu(\psi)}{[\lambda(\psi)+\mu(\psi)]^3}$$

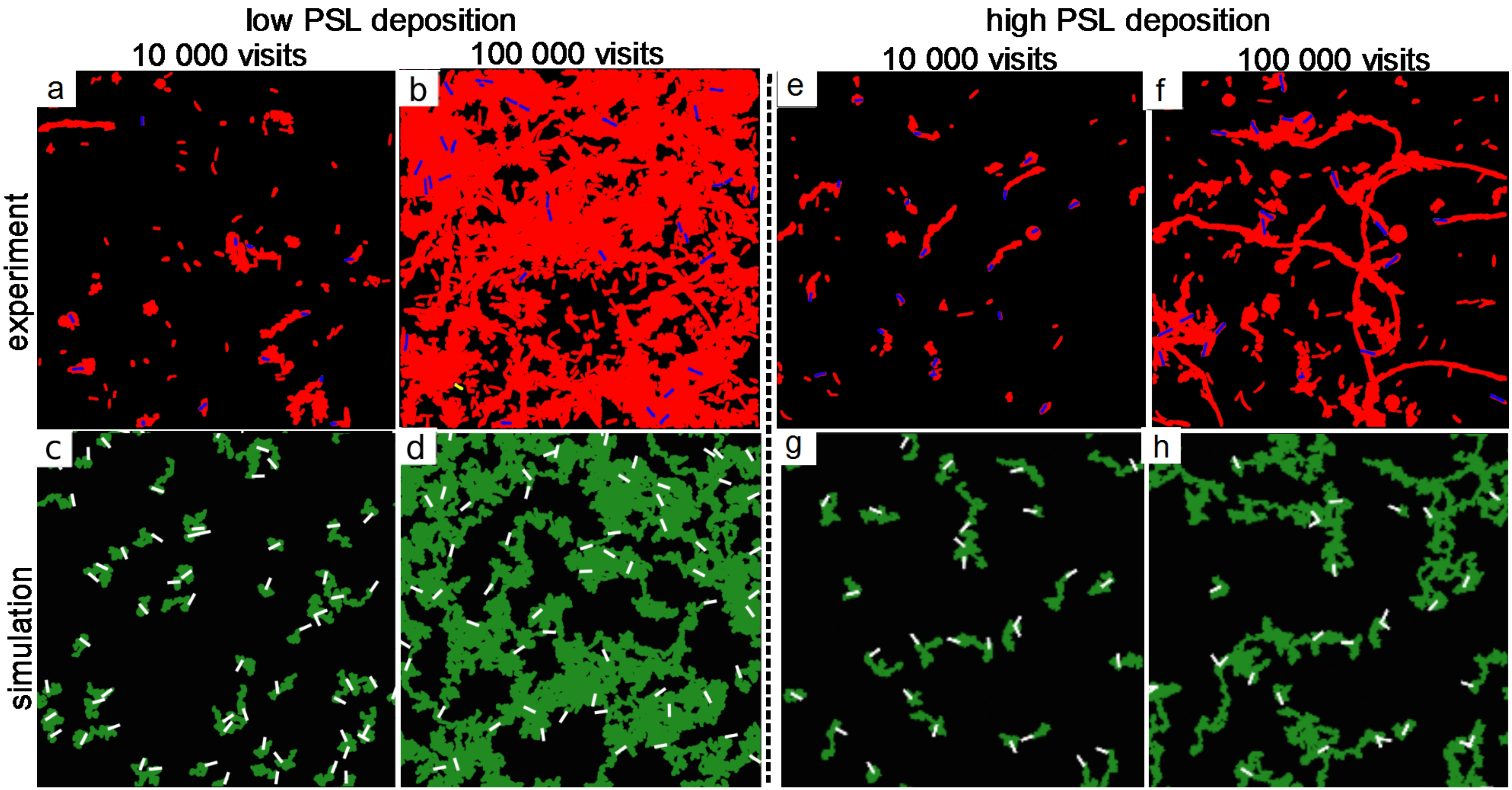
$$v(\psi) = N \langle \cos \vartheta_i \rangle \frac{f(\psi)}{\gamma_{||}} \frac{\lambda(\psi)}{\lambda(\psi)+\mu(\psi)}$$

non-trivial dependence on psl concentration due to competing contributions

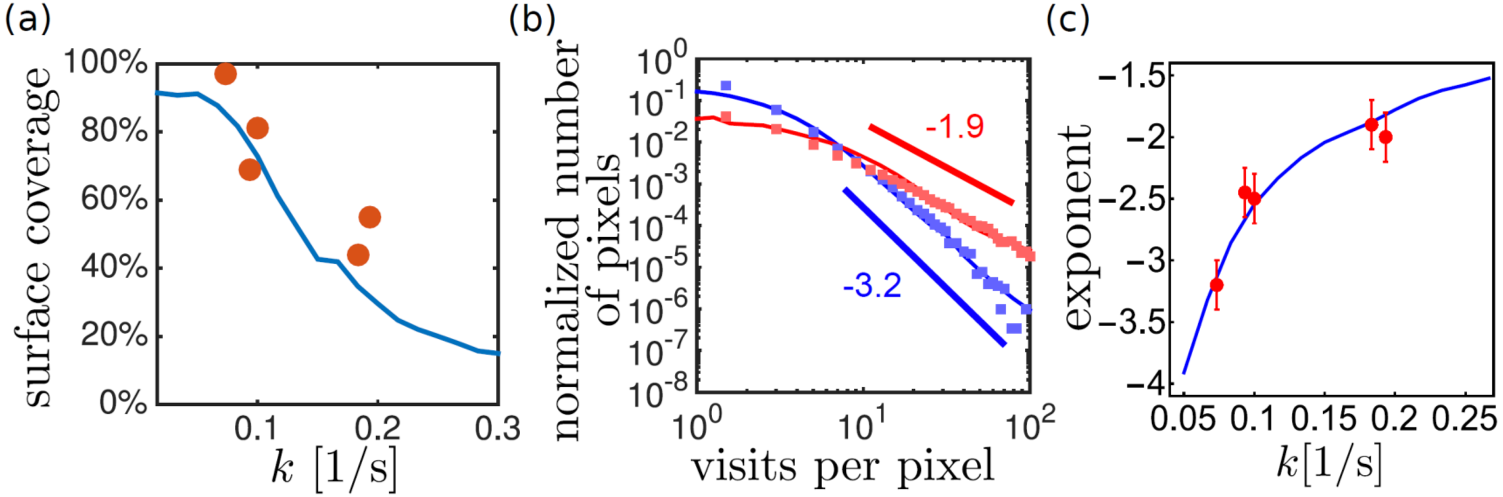
- **force increasing with psl**
- **friction increasing with psl**

- **attachment rate increasing with psl**
- **detachment rate decreasing with psl**

# Psl-dependent Self-Organization of *P. aeruginosa*



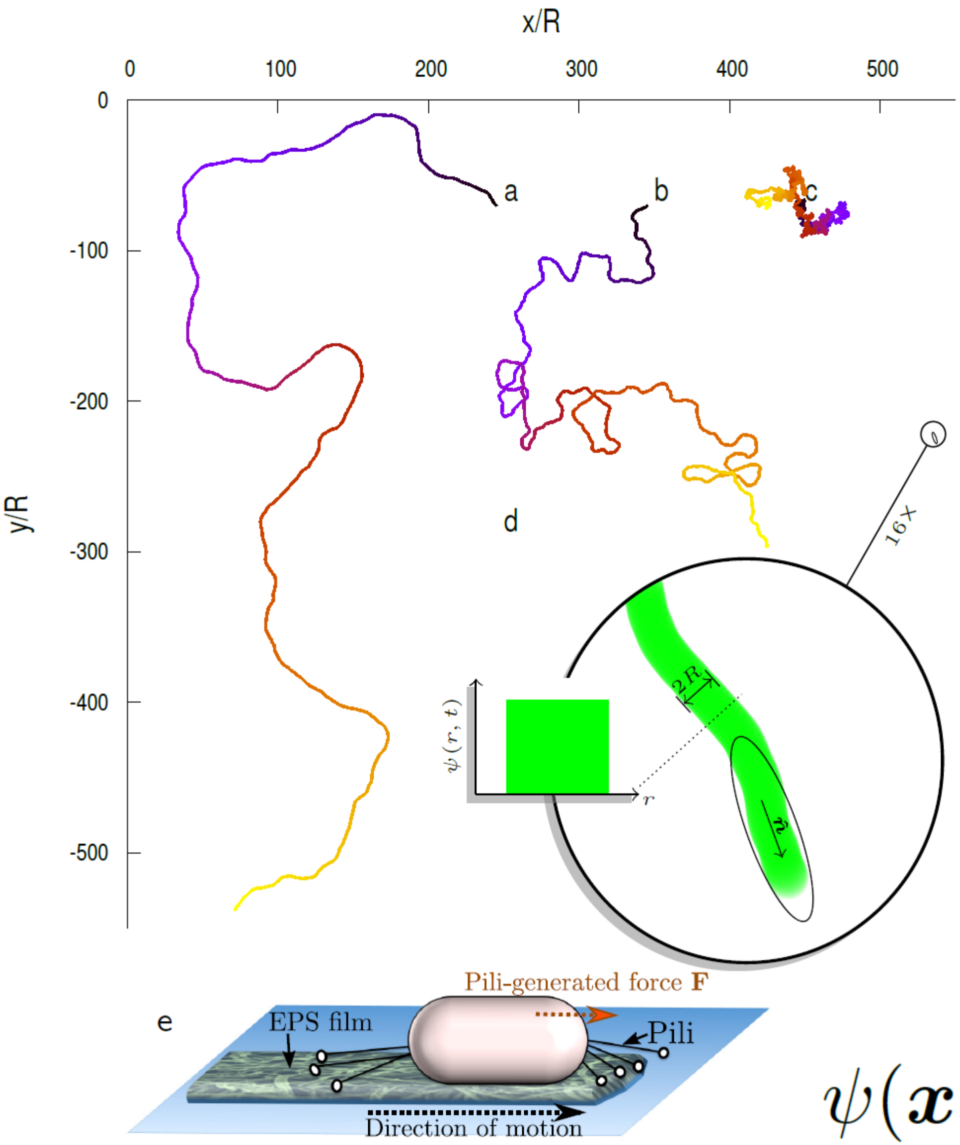
# Fractal Surface Visit Distribution




**Quantitative agreement without any fitting procedure**

**This verifies that the main ingredients in our single-bacterium model, and in particular the perpendicular alignment sensing mechanism, provide the correct phenomenology.**

# Phenomenology of Self-Trail Interaction




**Modulate trajectory:**

search a **larger** area
but **less** thoroughly

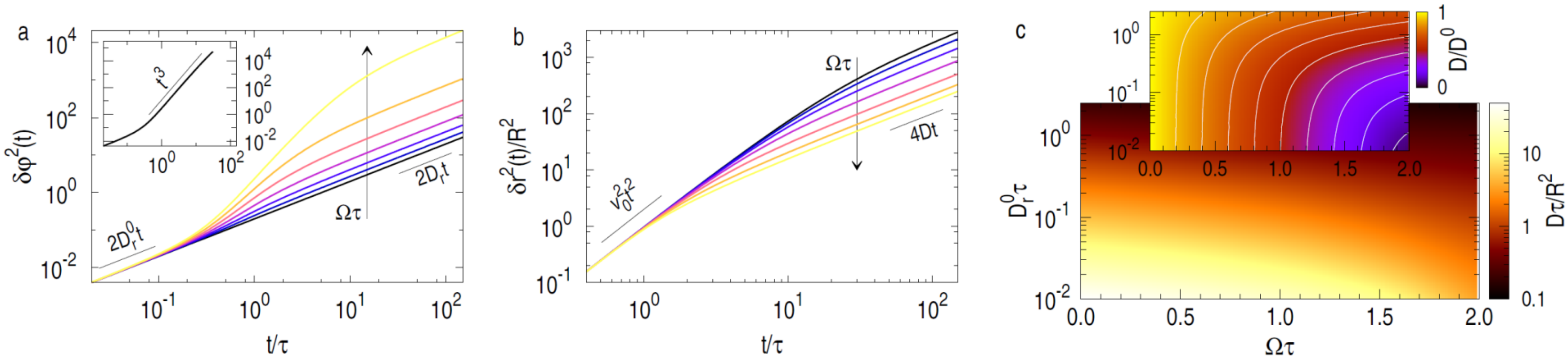
*versus*

search a **smaller** area
but **more** thoroughly

$$\psi(\boldsymbol{x}, t) = k \int_0^t dt' \, \delta_R^2 \left( \boldsymbol{x} - \boldsymbol{r}(t') \right)$$

W.T. Kranz, A. Gelimson, K. Zhao, G.C.L. Wong, and R. Golestanian, Phys Rev Lett **117,** 038101 (2016)

# Translational and Rotational Fluctuations




$$\frac{d\hat{\boldsymbol{n}}}{dt} = -\chi \hat{\boldsymbol{n}} \times (\hat{\boldsymbol{n}} \times \nabla \psi)$$

$$\boxed{\Omega = k\chi\tau/\pi R^3}$$

$$\tau = R/v_0$$

## Main characteristics of the motion:

- **super-diffusive orientational fluctuations**
- **diffusive translational motion with reduced diffusion**

# Nonlocality of Self-Trail Interaction

$$\partial_t \varphi(t) = \chi \partial_\perp \psi(\boldsymbol{r}(t), t) + \xi(t)$$

$$\partial_\perp \psi(t) \equiv \partial_\perp \psi(\boldsymbol{r}(t), t)$$

## Positive Feedback Mechanism

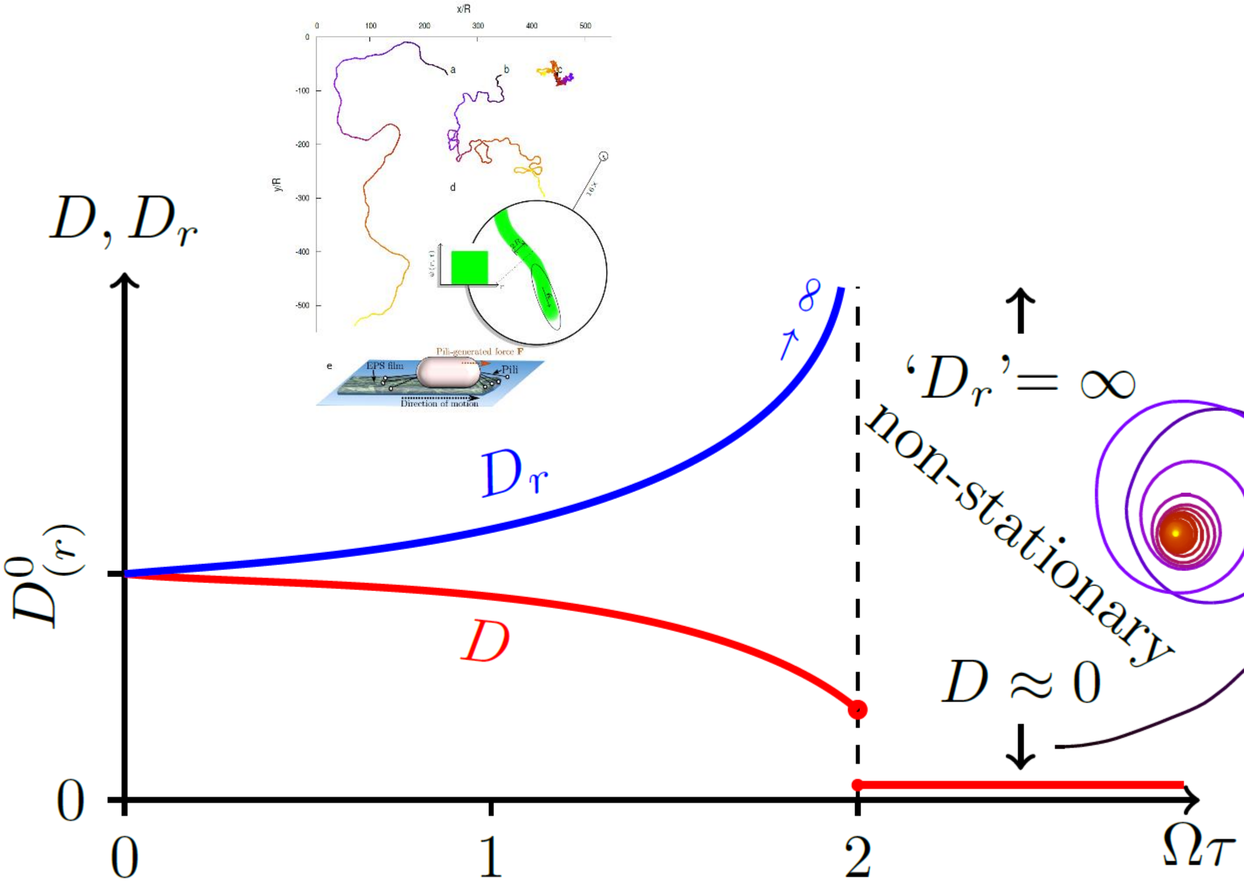
$$\partial_\perp \psi(t) = \frac{\Omega}{\tau} \int_0^\tau du\,(\tau - u)\,[\partial_\perp \psi(t-u) + \xi(t-u)/\chi]$$

$$\langle \partial_\perp \psi \rangle \sim \exp(\alpha t) \qquad \Omega = k\chi\tau/\pi R^3$$

$\Omega\tau < 2$ $\qquad \alpha < 0$

$\Omega\tau > 2$ $\qquad \alpha > 0$

# Dynamic Phase Transition




**discontinuous localization transition**

**with**

**simultaneously diverging rotational diffusion coefficient**

# Concluding Remarks

- Bacteria exhibit interesting behaviour near surfaces, and on surfaces, where they form dense colonies
- Polysaccharide trails are used by bacteria as a means of controlling their trajectories and signaling to others
- Bacteria align perpendicularly to the trails in order to be able to follow it (non-intuitive chemotaxis behaviour)
- Biofilm early colonies have a hierarchical structure

# Any Questions?